GENETIC VARIATION AND TAXONOMY OF THE LIZARDS ASSIGNED TO *CTENOTUS UBER ORIENTALIS* STORR (SQUAMATA: SCINCIDAE) WITH DESCRIPTION OF A NEW SPECIES

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Analysis of allozyme and morphological variation reveals that at least two scincid lizard species are presently confused under the trinomial *Ctenotus uber orientalis*. The status of *orientalis* is reassessed here with its elevation to a full species, while a new species is described from central South Australia, extending narrowly into adjacent areas of the Northern Territory, New South Wales and Queensland. This study reveals that significant genetic divergence has occurred within and between species groups of the large genus *Ctenotus*.

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Storr (1969) described *Ctenotus uber* from Western Australia as part of his initial taxonomic review of *Ctenotus*, Australia's largest genus of terrestrial vertebrates. In 1971 he described an eastern subspecies, *C. u. orientalis*, the only form recognised east of Western Australia. A third taxon, *C. u. johnstonei* was later described from northern Western Australia (Storr 1980). These taxa are all members of the *Ctenotus leonhardii* species group, one of several defined by Storr (1970, Storr *et al.* 1981, King *et al.* 1988) to aid identification. The phylogenetic relationships within and between Storr's species groups are yet to be studied.

There is considerable morphological variation in populations assigned to both of the widespread subspecies, *C. u. uber* and *C. u. orientalis*. The latter subspecies includes blackish, heavily spotted lizards, mostly distributed in the semi-arid to dry temperate woodlands of southern South Australia, Victoria and southern New South Wales, as well as populations of much plainer animals which inhabit arid chenopod and gibber habitats in the Lake Eyre basin through eastern South Australia to western New South Wales. Such apparent ecological and morphological plasticity is unusual in a single species and prompted us to question whether one or more cryptic species might be included within *C. u. orientalis* (Donnellan *et al.* 1993). It also led us to revisit the taxonomy of *orientalis* with respect to *uber*.

MATERIALS AND METHODS

We followed Storr (1969 *et seq.*), Greer (1982), King *et al.* (1988) and Hutchinson and Rawlinson (1995) in defining and describing morphological characters, such as scalation and proportions. Specimens examined were from the collections of the South Australian Museum, Adelaide (SAMA) and Western Australian Museum, Perth (WAM), and eastern Australian specimens in the Australian Museum, Sydney (AMS) and the Museum of Victoria, Melbourne (NMV).

Thirty-one specimens of South Australian *C. u. orientalis* were analysed for electrophoretic variation. These encompassed all of the morphological variation known and represented a wide geographical sampling. In order to assess the significance of any variation found, we also typed samples of three other morphologically similar South Australian species of *Ctenotus—C. leonhardii*, *C. regius* and *C. septenarius* (members of the *C. leonhardii* species group, Storr 1970). The morphologically distinct *Ctenotus strauchii varius* (*C. colletti* species group) was included as a more distant outgroup.

Our methods for allozyme electrophoresis using cellulose acetate gels ('Cellogel', Chemtron, Milan) follow Richardson *et al.* (1986). We scored the protein and enzyme products of 42 presumed loci for patterns of allelic variation. The proteins that were stained, abbreviations used and their Enzyme Commission numbers (International

Union of Biochemistry 1984) were: aspartate aminotransferase (AAT, EC 2.6.1.1), aconitate hydratase (ACOH, EC 4.2.1.3), acid phosphatase (ACP, EC 3.1.3.2), aminoacyclase (ACYC, EC 3.5.1.14), alcohol dehydrogenase (ADH, EC 1.1.1.1), albumen (ALB), carbonate dehydratase (CA, EC 4.2.1.1), diaphorase (DIA, EC 1.6.99.?), enolase (ENO, EC 4.2.1.11), esterase (EST, EC 3.1.1.?), fructose-bisphosphatase (FBP, EC 3.1.3.11), fumarate hydratase (FUMH, EC 4.2.1.2), ` glyceraldehyde-3-phosphate dchydrogenase (GAPDH, EC 1.2.1.12), glycerol-3-phosphate dehydrogenase (G3PDH, EC 1.1.1.8), glucose-6-phosphate dehydrogenase (G6PDH, EC 1.1.1.49), glucose-6-phosphate isomerase (GPI, EC 5.3.1.9), glutamate dehydrogcnase (GTDH, EC 1.4.1.3), 3-hydroxybutyrate dehydrogenase (HBDH, EC 1.1.1.30), L-iditol dehydrogenase (IDDH, EC 1.1.1.14), isocitrate dehydrogenase (IDH, EC 1.1.1.42), cytosol aminopeptidasc (LAP, EC 3.4.11.1), L-lactate dehydrogenase (LDH, EC 1.1.1.27), lactoylglutathione lyase (LGL, EC 4.4.1.5), malate dehydrogenase (MDH, EC 1.1.1.37), mannose-6-phosphate isomerase (MPI, EC 5.3.1.8), dipeptidase (PEP-A, EC 3.4.13.?), tripeptide aminopeptidase (PEP-B, EC 3.4.11.?), dipeptidase (PEP-C, EC 3.4.13.?), proline dipeptidase (PEP-D, EC 3.4.13.?), phosphoglycerate mutase (PGAM, EC 5.4.2.1), phosphogluconate dehydrogenase (PGDH, EC 1.1.1.44), phosphoglycerate kinase (PGK, EC 2.7.2.3), phosphoglucomutase (PGM, EC 5.4.2.2), purine-nucleoside phosphorylase (PNP, EC 2.4.2.1), superoxide dismutase (SOD, EC 1.15.1.1), and triose-phosphate isomerase (TPI, EC 5.3.1.1).

We based our initial analysis of the allozyme data on the null hypothesis that all samples stemming from a single panmictic species, which predicts genotype frequencies will conform to Hardy-Weinberg expectations. We examined multi-locus genotypes of individual skinks from a single locality for the Wahlund effect, a deficiency of heterozygotes from that predicted under Hardy-Weinberg expectations due to a sample with two or more genetically differentiated populations. The presence of two or more species in sympatry is often evident from the presence of fixed allelic differences at one or more loci where the genotypic classes are concordant among individuals (see Richardson *et al.* [1986] for a more detailed explanation). When we observed evidence of departure from Hardy-Weinbcrg expectations at one or more loci, individuals classified according to these multi-locus genotypes were treated as a population. Where no evidence of departure from Hardy-Weinberg expectations was observed, we treated all of the individuals at each of these locations as a population. Given our null hypothesis, this meant that in some cases we pooled distinct locations in the absence of genetic differentiation between the samples. We expressed phenetic diversity among populations using the Unweighted Pair-Group (UPGMA, Sneath & Sokal 1973) method. We also made a prcliminary assessment of the phylogenetic relationships of the populations studied using the Fitch-Margoliash method (Fitch & Margoliash 1967), based on Rogers' D, and a parsimony analysis, scoring the electromorphs using the method of Georges and Adams (1992). Software used for the analysis were the FITCH algorithm from Felsenstein's PHYLIP package, with input order randomised using the SHUFFL routine (25 passes), and the heuristic parsimony algorithm of Swofford's PAUP*.

RESULTS

The allozyme data identified 15 genotypic populations from among the specimens identified as *C. u. orientalis*, with 10 additional populations identified among the outgroup species (Table 1). Figure 1 shows the UPGMA phcnogram of the percentage fixed allelic differences between populations, while Fig. 2 shows a phylogenetic hypothesis for these populations based on the Fitch-Margoliash tree. The parsimony analysis produced the same topology.

The populations of *C. u. orientalis* fell into one of three clusters. Most belonged to two groups, one primarily southern and one primarily central, separated by a minimum of three fixed allelic differences at the *Adh, Dia* and *Pep-A* loci. A third group, is represented by the single specimcn from Arrabury, Qucensland which has a minimum of three fixed (or almost fixed) allelic differcnces at thc *Acoh, Pep-B* and *Sod-1* loci compared with the other two groups. Our sampling is not adequate to examine geographic patterns of variation within each cluster but the presence of some within-group allelic variation suggests that future, more detailed sampling would yield useful information.

Ctenotus leonhardii, *C. regius*, and *C. septenarius*, also members of the *C. leonhardii* species group, wcre distinct from the three *C. u. orientalis* groups and from *C. strauchii varius*. Interspecific levels of genetic divergence within the *C. leonhardii* group ranged from an average
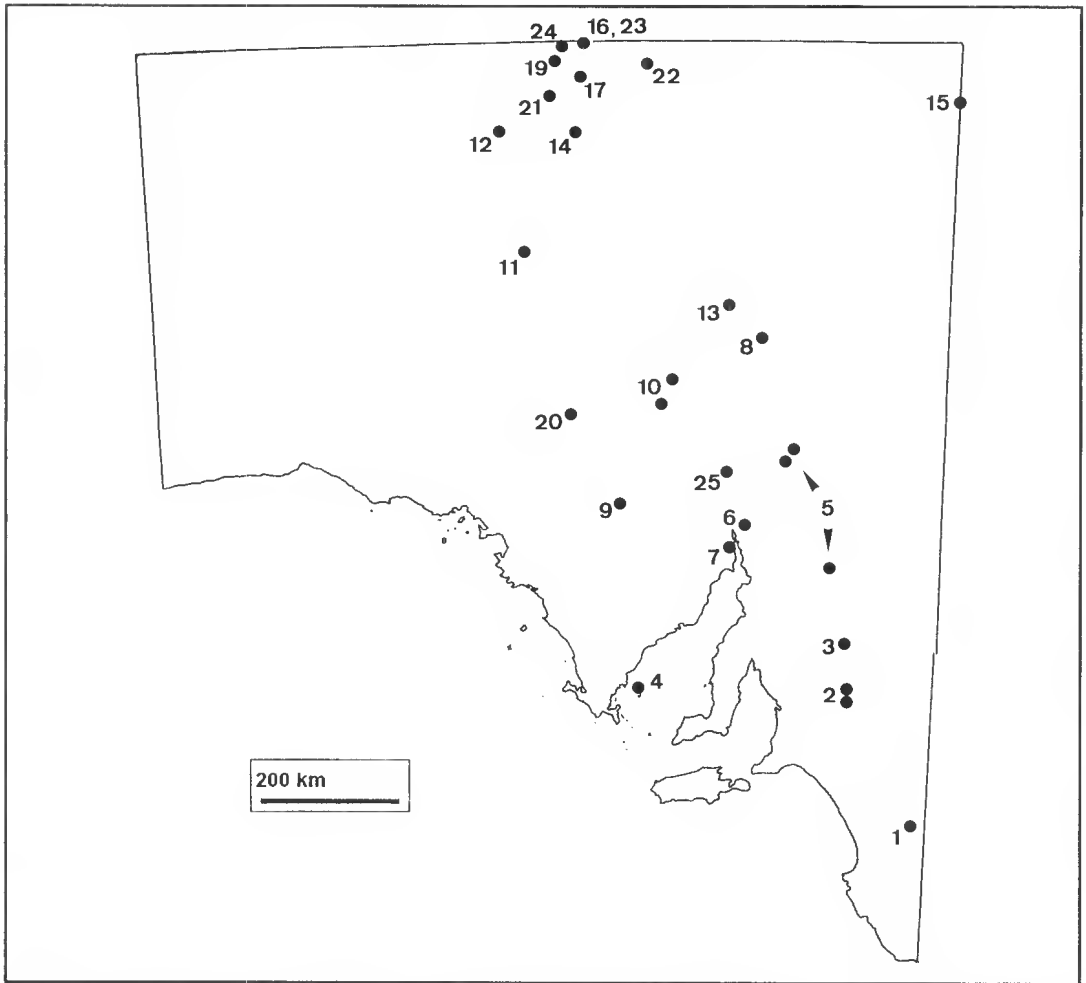
FIGURE 1. Map of South Australia showing the geographic origin of the populations sampled for allozyme data. See appendix for details of localities and specimens.

of 9% fixed differences between 'southern' and 'central' *C. u. orientalis* to 20% between *C. leonhardii* and the other species group members. As expected, *C. s. varius* was the most divergent taxon, with an average of 34% fixed allelic differences compared with any member of the *C. leonhardii* species group.

The three genetic groups within *C. u. orientalis* can be distinguished morphologically. The 'southern' group is identical to the holotype of *C. u. orientalis*. The pale dorsolateral stripe is prominent and continuous, the black laterodorsal stripes have straight medial edges and completely enclose single series of pale dots or short dashes and there is always a light-edged, black vertebral

stripe. The lateral pattern consists of two to four series of small white dots, bordered below by a white midlateral stripe which is continuous posteriorly but which normally breaks up well before reaching the axilla.

The 'central' group has variable development of a light dorsolateral stripe and the black laterodorsal stripes are absent or ragged-edged medially; if a laterodorsal series of pale dots is present, the spots are not completely surrounded by blackish background colour, but contact the light laterodorsal region. The dorsum is usually metallic medium brown with a black vertebral stripe which lacks distinct pale edges. The lateral pattern is similar to that of the 'southern' group.

TABLE 1. Allele frequencies at 31 loci, expressed as a percentage, in 25 populations of *Ctenotus*. Alleles are designated alphabetically, with a being the most cathodally migrating allele. Where enzymes are encoded by more than one locus, the loci are designated numerically in order of increasing electrophoretic mobility. Where the allele frequencies are not given, the frequency is 100. The number of individuals sampled is indicated in parentheses. The following 11 loci were invariant: *Enol, Fdpase, Gapd, Gdh, Got-1, Gpi, Ldh-1, Mdh-1, Mpi, Np* and *Pgam*.

	Species 1								Species 2						Species 3	*septenarius*		*leonhardii*			*regius*			*strauchii*	
Locus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
	(1)	(5)	(1)	(5)	(3)	(1)	(1)	(1)	(4)	(4)	(1)	(1)	(1)	(1)	(1)	(5)	(1)	(1)	(2)	(1)	(2)	(1)	(1)	(3)	(1)
Acon	c	d(30) c(70)	c	d(30) c(70)	c	c	e(50) c(50)	c	c	d(50) c(50)	c	c	c	c	d	d(30) c(70)	c	d	d	d	b(25) a(75)	b(50) a(50)	c(50) b(50)	d(50) c(50)	c
Acp	b	b	b	b	b(83) a(17)	b	b	b	c(50) b(50)	b	b	b	b	b	b	b	b	b	c(25) b(75)	-	b	b	b	b	b
Acyc	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	-	a	a	a	a	a
Adh	a	a	a	a	b(17) a(83)	c(17) a(83)	c(50) b(50)	c(50) b(50)	b	b	b	b	b	b	b	b	b	d(50) c(50)	d(50) c(50)	c	b	b	b	e(17) d(83)	d
Alb	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b		a
Ca	a	b(10) a(90)	a	a	a	a	b(50) a(50)	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Dia	c	d(20) c(80)	c	c	c	c	b	b	b	b	b	b	b	b	c	a	a	b	b	b	b	b	b	e	f(50) e(50)
Est	b	b	b	b	b	b	b	b	b(75) a(25)	b(87) a(13)	b	b	b	b	b	c(10) b(90)	c(50) b(50)	b	c(25) b(75)	b	b	b	b	b	b
Fum	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	c
Glo	a	a	a	b(20) a(80)	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
Got-2	a	a	a	a	b(17) a(83)	a	a	a	b(25) a(75)	a	a	a	a	a	b(50) a(50)	a	a	a	a	b(50) a(50)	a	a	a	a	a
G6pd	b	b(90) a(10)	b(50) a(50)	a	b	b	b	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b
Gpd	c	c(90) b(10)	c	c	c(83) b(17)	c	b	b	c(16) b(67) a(17)	c(12) b(88)	c(50) b(50)	c(50) b(50)	b	b	b	b	b	b	b	b	b	b	b	d(17) c(83)	c
Gpi	b	b	b	b	b	b	b	b(75) a(25)	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a

	Hbdh	Idh-1	Idh-2	Lap	Ldh-2	Mdh-2	PepA	PepB	PepC	PepD	6Pgd	Pgk	Pgm	Sod-1	Sod-2	Sordh	Tpi
	c	b	a	b	a	a	b	b	c	d	d	a	a	a	a	c(50) a(50)	a
	c	b	a	b	a	a	c(17) b(83)	c(17) b(83)	c	e(33) d(50) a(17)	f(17) d(83)	a	b(17) a(83)	a	a	a	a
	b	b	a	a	a	b	c	b	b	b	d	b	a	c	g	g	b
	b	b	a	a	a	b	d(25) c(75)	b	c(50) b(50)	b	d(50) a(50)	b	a	c	g	g	b
	b	b	a	a	a	b	d(25) c(75)	b	c(50) b(50)	b	d	b	a	c	g	g	b
	b	b	a	a	a	b	b(50) a(50)	b	b(50) e(50)	e	d	b	a	c	b	c	c
	c	b	a	a	a	b	c(20) b(80)	b	b	a	d	b	a	b	b	c	c
	b	b	a	a	a	b	b(50) a(50)	b	a	e	d(50) b(50)	b	a	c	b	c	c
	b	b	a	a	a	b	b	b	a	f(75) e(25)	d	a	b	c	b	b	b
	a	b	a	a	-	a	a	a	b	e	e	b	a	c	a	g	b
	b	b	a	a	a	b	d(50) c(75)	b	c(50) b(50)	d(87) c(13)	d	b	a	c	a	c	b
	b	b	a	a	a	a	c(37) b(63)	c(62) b(38)	c(12) b(88)	d	d	b	a	a	a	g	c
	b	b	a	a	a	a	c(50) b(50)	b	b	d	e(12) d(75) a(13)	a	a	a	a	h(12) f(50) d(25) c(13)	c
	b	b	a	a	a	a	b	a	b	b	d	a	b	a	a	d(12) c(75) b(13)	c
	b	b	a	b(25) a(75)	a	a	a	a	b	a	d	b	a	a	a	c	c
	a	b(90) a(10)	a	a	a	b	f(50) d(50)	d(50) c(50)	b	d	d(50) d(50)	b	a	a	a	d(50) c(50)	c
	b	b	a	a	a	b	e(17) d(83)	d(50) c(50)	b	d	f(50) d(50)	a	a	a	a	c	c
	b	b	a	a	a	b	e(17) d(83)	c(50) b(67)	b	e(17) d(83)	d	a	a	a	a	c	c
	b	b(90) a(10)	a	a	a	b	c(40) b(50)	c(40) b(60)	b	e(17) d(83)	d	a	a	a	a	e(17) d(33) c(50)	c
	b	b	a	a	a	b	d(50) b(60)	c(33) b(67)	b	d(50) c(50)	d	a	a	a	a	c(20) b(30) a(50)	c
	d(10) b(90)	b	b(50) a(50)	a	a	a	f(50) d(50)	d(50) c(50)	c(40) b(60)	d(50) c(50)	d(70) c(30)	a	a	d(50) a(50)	a	c(50) b(30) a(20)	c
	b	b	a	a	a	b	d	a	c	d	d	a	a	a	a	c	c

FIGURE 2. Phenogram of percentage fixed differences, constructed by UPGMA, for 25 populations of *Ctenotus* species.

The single specimen from Arrabury is heavily speckled dorsally and laterally, but with weakly contrasting dorsal stripes, the upper lateral and laterodorsal stripes being medium brown rather than blackish. The light dorsolateral stripe consists of dark-edged, light-centred scales and is indistinct due to the presence of other pale-centred scales which pattern the laterodorsal and upper lateral zones.

Two cases of syntopy are known, from the Flinders ranges (AMS R60053–54, 21 km S of Copley, P. Rankin & G. Husband, 22 January 1977) and the Olary Spur (SAMA R13156, R39266, near Oulnina homestead, R. Forsyth, 1 April 1972), and the distributions of the 'southern' and 'central' groups abut or overlap in the Gawler Ranges, Flinders Ranges and on the Olary Spur. There is no suggestion in the morphology or the allozyme data of clinal or other variation which might indicate genetic continuity between the two groups, while the groups maintain internal genetic uniformity over wide geographic ranges.

Typical *C. u. uber* was not available for electrophoretic comparisons, but it represents a fourth and highly distinctive morphological group, characterised by rufous rather than grey-brown dorsal colouring, different pattern details and longer tail (see also Storr 1971). *Ctenotus u. uber* itself encompasses considerable morphological variation. The ranges of *C. u. uber* and 'southern' group do not contact but no obviously intermediate specimens or populations are known. There seems to be no grounds for assuming, as Storr's taxonomy implied, that *uber* and *orientalis* are genetically continuous or even sister taxa.

At least three of the four taxa discussed here, *C. uber* and the 'southern' and 'central' groups of *C. u. orientalis* are species. The distinctive morphology, together with multiple concordant fixed allelic differences at allozyme loci (in the case of *C. u. orientalis*), and lack of intergradation indicate that reticulate evolution has ceased between populations of the different groups, which are therefore on their own evolutionary trajectories (Frost & Hillis 1990). The Arrabury specimen we leave indeterminate at present, as its taxonomic treatment will undoubtedly involve other poorly understood populations and nominal species from the eastern inland of Australia. Further work is also needed to address the taxonomic problems posed by the considerable variation that exists within Western Australian *C. uber*, including the status of *C. u. johnstonei*.

Taxonomy

All of the following species are members of the *Ctenotus leonhardii* species group, defined originally by Storr (1970) and subsequently modified by Storr *et al.* (1981) and King *et al.* (1988). The latter authors defined the C. *leonhardii* species group in part by two colouration characteristics, a predominance of reddish rather than olive pigmentation, and the replacement of black by dark brown pigmentation. Neither of these is true for all species; indeed, the second is scarcely true for any! In addition, the toes are said to be distinctive in being compressed, with subdigital lamellae tipped by obtuse keels or narrow to moderately wide calli. This characteristic is generally true for all species we have examined, but leaves considerable leeway for observer bias and confusion in applying the definition to particular specimens. Species groups, and more particularly phylogenetic groups, within *Ctenotus* need to be redefined as lineages rather than (as at present) being merely tools to simplify identification.

Ctenotus uber Storr, 1969

Ctenotus uber Storr, 1969, p. 102. Holotype: WAM R17654, 22 miles SE of Yalgoo, WA [approx. 28° 35' S, 116° 26' E].

Diagnosis

Ground colour of body reddish orange. Black vertebral stripe very narrow (occupying no more than the median one-quarter of each vertebral scale row) or absent. Laterodorsal dark brown to black stripes bearing a series of distinct pale spots. Original tail averages more than 200% of snout-vent length (SVL).

Description

Storr's (1969) description of scalation and proportions is not significantly altered by the larger sample now available for examination. Midbody scales in 28–33 rows, the mean of 30.2 ($\pm$1.19), based on a sample of 52 specimens, is very close to Storr's figure of 30.8. The value for relative tail length, reported by Storr to average 222% of SVL based on eight specimens, is comparable to the value of 216% ($\pm$44.6) obtained by us, based on Storr's specimens plus a further 27 specimens. Nasals almost always separated (frequency = 0.96). Prefrontals usually separated (frequency = 0.63). Storr's data (1971) suggested
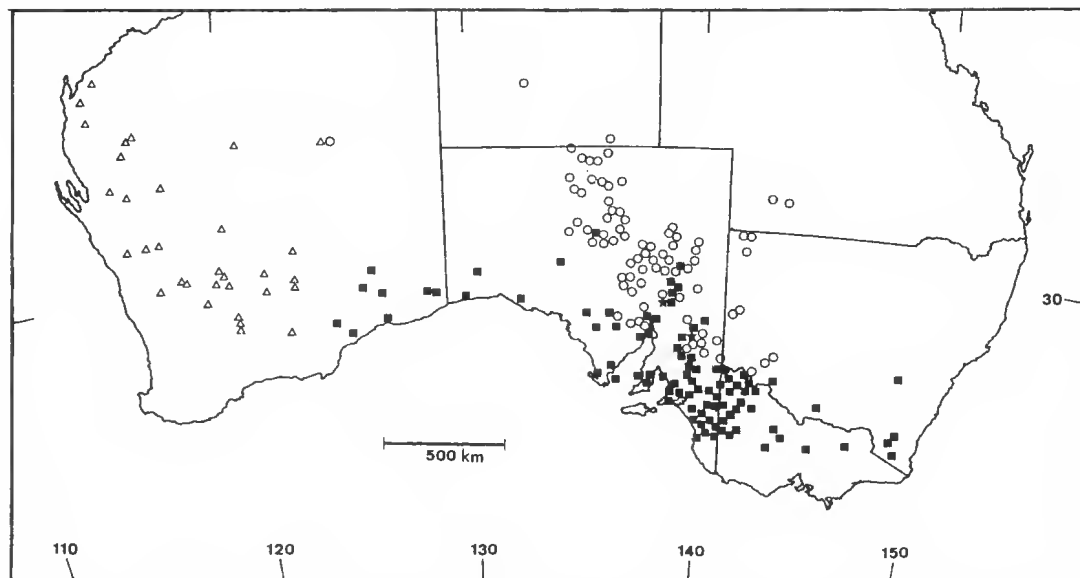
FIGURE 3. Geographic distributions of *Ctenotus uber* (Δ), *C. orientalis* (■) and *C. olympicus* (○). Stars indicate two instances of syntopy of *C. orientalis* and *C. olympicus*.

that loreal proportions could help differentiate *uber* and *orientalis*, but our measurements indicate that the two species are very similar in this respect; posterior loreal length/height ranges 0.8–1.6 in both species, and mean values are 1.2 (±0.17) for *C. uber* and 1.1 (±0.18) for *C. orientalis*.

Colour is medium reddish to orange brown on the dorsal surface of the head, limbs and tail. Laterodorsal and dorsolateral zones black, divided by a pale brown to whitish dorsolateral line. A narrow black vertebral stripe may be present or absent. Laterodorsal dark zone with a single longitudinal series of pale brown to whitish spots. Upper lateral zone demarcated ventrally by a midlateral white stripe beginning in the inguinal region, but breaking up anteriorly (about midway to forelimb) into a series of whitish spots. Upper lateral zone bearing several series of small whitish dots. Lower lateral zone variable, with irregular grey ventrolateral blotching or spotting.

Colour photograph in Storr *et al.* (1981).

Distribution

Western Australia, from the Exmouth Gulf area, south and east as far as the edge of the Nullarbor Plain. Southeastern limits roughly along the line connecting Mullewa–Lake Hillman–Parker Range–Norseman. Northeastern limit poorly

defined but few specimens have been recorded northeast of a line connecting Dampier and Rawlinna.

Notes

Storr's type series included specimens now assigned to other species: *C. orientalis* (WAM R17268, R17284–85) from the Nullarbor Plain and *C. septenarius* (R20759) from the Rawlinson Range. Three specimens, from Mungilli Claypan (R26894–5) and 18 km E of Mungilli Claypan (R26897, i.e. the vicinity of Mt Johnston at the northern end of the Fame Range), are also not typical *C. uber* and are considered further in the 'Discussion' section below.

Ctenotus uber is mostly confined to the west and southwestern interior of Western Australia. There is marked geographic variation in colour pattern. The pattern which conforms most closely with Storr's original description is that of the holotype, in which the zone of dorsal ground colour along the vertebral region, which separates the laterodorsal zones, is narrow, occupying no more than half a paravertebral scale on each side, but almost always includes a dark vertebral stripe (sometimes fading on the posterior one-third of the dorsum). In south-central Western Australia, this 'median strip' of rufous colouring is often much wider, occupying up to one paravertebral

scale on each side, narrowing the laterodorsal zones so that the laterodorsal series of spots almost contact the middorsal colour, and there is usually little or no trace of a dark vertebral stripe posterior to the shoulder region. Northwestern specimens, from about the latitude of Shark Bay northwards, are generally paler with more pronounced spotting and less contrasting dorsolateral stripes.

Ctenotus orientalis Storr, 1971

Ctenotus uber orientalis Storr, 1971, p.8. Holotype: NMV D825, Ouyen, Victoria [35° 04' S, 142° 19' E].
Minervascincus monaro Wells and Wellington, 1985, p. 35. Holotype: AMS R92239, 6 km along Cambalong Rd, Bombala, New South Wales (36° 53' S, 149° 08' E).

Diagnosis

Ground colour of body beige to medium brown, without reddish tinge. Black to dark chocolate or dark reddish brown laterodorsal zone generally reduces exposure of the ground colour to a pair of paravertebral lines and a series of pale dots or dashes within each laterodorsal dark zone. Black to dark brown vertebral stripe always present and usually occupying about one-third of each vertebral scale row. A pale brown to white dorsolateral stripe always present and straight-edged.

Description

Storr's original description was based on few specimens and on a composite type series (see below). Examination of a series of 31 South Australian specimens results in the following redescription.

Midbody scales in 30–35 rows (mean 32.3±1.49). Nasals usually separated (frequency = 0.77). Prefrontals separated (frequency = 0.58) or in contact. Supraoculars 4, the first three in contact with the frontal. Supraciliaries 6–8, mode 7. Second (posterior) loreal 0.8–1.6 (mean 1.2) times as wide as high. Supralabials 8, with occasional asymmetric presence of 7 or 9. Ear lobules 4–6, variably shaped and proportioned, but generally obtusely pointed and with the second (from the top) the largest. Lamellae under fourth toe 20–27 (mean 23.9± 1.64), slightly to moderately compressed, each with a dark brown callus.

Adults (sexes similar): SVL (n = 26) 56–82

mm; hindlimb length (n = 26) 28–39 mm (41–57% SVL); tail length (n = 12) 109–158 mm (168–223% SVL, mean 171%±55.2).

Head, limbs and tail light grey-brown to tan. Body usually best described as black to dark brown with a pair of narrow, straight-edged pale brown paravertebral lines separating a dark vertebral stripe from the dark laterodorsal zones (Fig. 4A). The vertebral stripe occupies about one-third of each paravertebral scale row and terminates on the base of the tail. Each laterodorsal dark zone contains a single series of pale brown spots or short dashes. Light dorsolateral stripe well-developed, straight-edged. Upper lateral zone blackish, enclosing numerous small off-white dots, arranged roughly in two to four longitudinal series. A whitish midlateral stripe begins in the groin and runs anteriorly to about two-thirds of the axilla-groin distance, where it breaks up, becoming indistinguishable in the axillary region. Tail and limbs light grey-brown to yellowish-brown, the colour sometimes extending anteriorly along the posterior third of the back, between the vertebral and laterodorsal dark stripes. Dorsolateral dark zone extends along the tail as a dark brown lateral stripe. Ventral surface pearly white in life.

Colour photographs in Jenkins and Bartell (1980, p. 137), Knowles and Wilson (1988, fig. 413) and in Cogger (1996, p. 448).

Distribution

Southern semi-arid to dry temperate Australia from the Nullarbor Plain in Western Australia across southern South Australia (north to Anna Creek), through northwestern Victoria and the far south of New South Wales. Scattered populations extend further east into dry woodlands of the Great Dividing range in northeastern Victoria, southeastern New South Wales and the Australian Capital Territory.

Notes

Storr (1971) described *orientalis* as a subspecies of *uber*, presumably on the basis of the shared dorsal pattern of laterodorsal spots and heavily spotted flanks. Since then other spotted-backed *Ctenotus* have been recognised or redescribed, so that the shared colour pattern is no longer unique to these two species. We separately assessed morphological variation in a sample of 23 Western Australian *C. orientalis* to see if any trends suggested intergradation with *C. uber*. None was apparent. Western Australian *C. orientalis* are if anything more different from *C.*

uber in colour pattern than eastern *C. orientalis*, with less contrast between the light and dark hues, and the tail shorter (mean 166 % SVL, ± 8.4%, n = 9).

Peterson and Shea (1987) reassessed Peters' description of *Lygosoma schomburgkii*, redefined as *Ctenotus schomburgkii* by Storr (1969), which has a mixed syntype series, including both *schomburgkii* and *uber orientalis, sensu* Storr (1969, 1971). Peterson and Shea concluded that Peters' description applied strictly to the larger taxon, i.e. Storr's *uber orientalis*, which should therefore bear the name *schomburgkii* with nomination of a new lectotype. Storr (1987) in reply asserted that the description was more ambiguous than suggested by Peterson and Shea and that, in his opinion, Peters' description was composite. Peters' description of *schomburgkii* would most likely apply to Storr's *uber orientalis*, but Storr's notion of a composite type description by Peters remains reasonable; his usage as first reviser, and lectotype designation, is accepted here.

Storr's type series of *uber orientalis* is itself composite, including specimens now recognised as *orientalis* (NMV D00825, SAMA R0023–24, R01507, R05738, R10122), *olympicus* sp.nov. (SAMA R02789, R09466–69, R10017, R10027, R10030, R10044, R10055) and *septenarius* (SAMA R09735). Our redefined *C. orientalis* shows one major pattern of geographic variation, with most specimens from the Nullarbor Plain being markedly lighter coloured, with the laterodorsal and upper lateral zones being medium to dark reddish brown rather than black, reducing the contrast between the light and dark dorsal colours. Note that this variation does not imply intergradation with *C. uber*, as the rufous colouring of the latter species is confined to the lighter areas while upper lateral and laterodorsal colour is strongly contrasting black. Some southeastern Australian specimens have only a single series of rather large pale spots in the upper lateral zone and a more continuous midlateral stripe.

Minervascincus monaro Wells and Wellington, 1985 is based on a New South Wales specimen of *C. orientalis*. The authors provided no description of the holotype specimen or the species, nor any differential diagnostic data. They declared the species to be 'readily identified' by the photograph in Jenkins and Bartell (1980, p. 137), and that it was 'clearly evident' that the illustrated animal was not *C. uber*, but made no comparison with *C. orientalis*. Examination of both the holotype and the cited photograph shows the colour and pattern are completely concordant with typical *C. orientalis*, although the holotype specimen does have an unusually low midbody scale count of 28. It also has the less common condition of two other head scale attributes, nine supralabials and the nasals in contact.

Ctenotus orientalis occurs in a variety of warm-temperate to semi-arid woodland and heathland habitats, including open forest, woodland (including mallee) and low shrubland. It occurs patchily in the more heavily wooded areas, confining itself to especially dry or exposed microhabitats. It is syntopic with *C. robustus* through most of its range, but also occurs with *C. regius* in drier areas. From both it is distinguished by the presence of dorsal spotting and the incomplete pale lateral stripe. These lizards usually build their own burrows in sandy soil or under rocks.

Three specimens (AMS R59784–6) registered as *C. u. orientalis* from the western slopes of the Dividing Range in New South Wales, in the Cassilis area, are distinctive in colouration and from outside the range of typical *orientalis*. These are excluded from the distribution map, and for now their identification is left as indeterminate.

Ctenotus olympicus sp. nov.

Holotype: SAMA R20949, male, 48 km S of Olympic Dam, SA, 30° 48' S 136° 52' E.

Paratypes: 13 specimens from South Australia: SAMA R18620, approx. 20 km S of Port Augusta, 32° 38' S, 137° 35' E; R20936, Olympic Dam area, 30° 19' S, 136° 57' E; R20944–45, 48 km S of Olympic Dam, 30° 48' S, 136° 52' E; R25877, Witchelina Station, near homestead, 30° 01' S, 138° 03' E; R28203, 37 km N of Oodnadatta on road to Hamilton homestead, 27° 15' S, 135° 17' E; R28494, 118.5 km NE of Minnipa, 32° 15' S, 136° 14' E; R28503, 119.3 km NE of Minnipa, 32° 18' S, 136° 16' E; R28517, 115–120 km NE of Minnipa, 32° 20' S, 136° 17' E; R28543, 115 km NE of Minnipa, 32° 16' S, 136° 11' E; R30407, Breakaways Reserve, 25 km NNW of Coober Pedy, 28° 50' 40" S, 134° 41' 15" E; R35937, 95 km E of Marla, 27° 09' S, 134° 21' E; R36360, 1 km NE of Alberrie Creek, 29° 37' S, 137° 33' E.

The type series is restricted to the specimens used in the electrophoretic analysis.
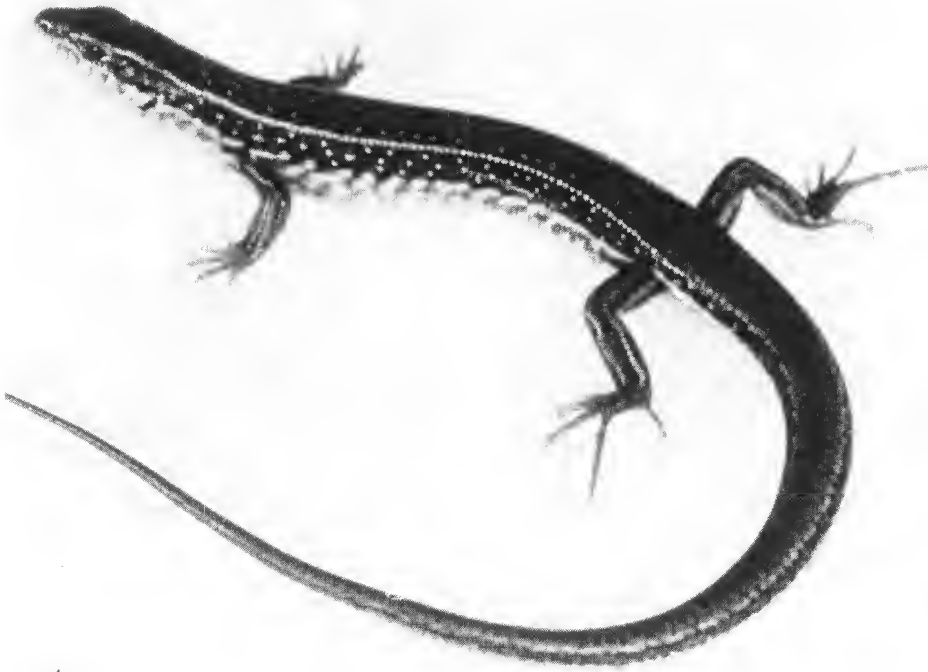
FIGURE 4. (A) *Ctenotus orientalis* from Whyalla, SA. (B) *C. olympicus* from the Davenport Range, SA. Photographs: T. Peters, SA Museum

Diagnosis

A member of the *C. leonhardii* species group with the dorsal ground colour pale beige to medium brown, often with a metallic lustre. Black vertebral stripe usually present, occupying no more than one-quarter of each paravertebral scale row and with very weak or no pale edging. Laterodorsal dark brown to black stripes, if present, with medial margins irregular, broken up by scattered lighter centred scales. Light dorsolateral line present or absent. Midlateral white stripe, if present, not extending anteriorly beyond midbody and often completely reduced to a zone of whitish spots. Size relatively small, SVL usually less than 70 mm; tail moderate (mean 187% SVL).

Description.

Based on type series (n = 14). Midbody scales in 28–32 rows (mean 30.9). Nasals usually separated (frequency = 0.64). Prefrontals usually in point to broad contact (frequency = 0.64) or separated. Supraoculars 4, the first three in contact with the frontal. Supraciliaries 7, rarely 6 or 8. Second loreal 0.8–1.6 (mean 1.2) times as wide as high. Supralabials 8, with occasional asymmetric presence of 7 or 9. Ear lobules 4–6, mostly obtusely pointed, the second or third (from the top) the largest. Lamellae under fourth toe 23–29 (mean 26.2), slightly to moderately compressed, each with a dark brown callus.

Adults (sexes similar; n = 13): SVL 52–69 mm; hindlimb length 26–35 mm (45–59% SVL); tail length (n = 11) 98–137 mm (170–211% SVL, mean 191%).

In preservative light brown, golden or medium brown dorsally. A narrow black vertebral stripe almost always present, occupying the corners of the paravertebral scale rows and no more than one-quarter of a paravertebral scale in width, runs from the nape to the base of the tail (Fig. 4B). This stripe sometimes poorly contrasting with dorsal colour and with no, or only a weakly contrasting, pale edge. A cream dorsolateral stripe, bordered medially by black, begins behind the supraciliaries. The posterior extent of this stripe is variable, sometimes continuing as far as the hips, but more often breaking into a zone of light and dark spots between forelimbs and hindlimbs. In specimens with a more continuous light dorsolateral stripe, the dark medial border (laterodorsal stripe) is usually narrow with a ragged medial edge. This stripe may include pale spots as in *C. orientalis* but in these cases the dorsolateral light stripe is often poorly defined

posteriorly due to the adjacent dark areas being heavily speckled with whitish. Upper lateral zone blackish, with three to four longitudinal series of small, irregular pale spots. Upper lateral zone continues along the sides of the tail as a brown lateral stripe irregularly dotted with black. Lower border of upper lateral zone demarcated by a series of pale spots and dashes, sometimes forming an irregular midlateral stripe posteriorly. Lower lateral zone whitish irregularly smudged with grey. Ventral surface white. In life hind limbs and tail have a reddish tinge.

Examination of an additional 35 referred specimens in the SAMA collection indicates that the above counts and measurements are representative. In the larger sample, midbody scales averaged 30.4, frequency of separated nasals was 0.60 and of prefrontals in contact, 0.66. Maximum SVL was 75 mm (SAMA R03618, male, one of the paratypes of *C. u. orientalis*).

Etymology

Named for Olympic Dam, the type locality, but also in the spirit of the Greek mythological bent behind many *Ctenotus* specific epithets.

Distribution

Lake Eyre and Lake Torrens basins of central and northern South Australia, extending northwards into the southern NT and east and south through the northern Flinders Ranges to the Olary Plains of eastern South Australia and the adjacent west of New South Wales.

Notes

Three species of the *C. leonhardii* group are superficially similar to *C. olympicus* and are sympatric or parapatric through significant parts of its range. *Ctenotus orientalis* differs in having a pale margin to the black vertebral stripe and straight-edged black laterodorsal stripes completely enclosing a single series of pale dots or dashes. *Ctenotus septenarius* has a rusty orange dorsal colour with contrasting yellowish tail, multiple dark dorsal lines anteriorly and a well-developed midlateral stripe. *Ctenotus leonhardii* lacks laterodorsal pale spots, has a pale-edged vertebral stripe, straight-edged, light dorsolateral stripe and distinctive cheek and neck pattern of white spots on a purplish-brown background.

Most populations include a range of colour pattern variations, but plainer animals are more common in the west of the species' range while more heavily speckled animals are more common
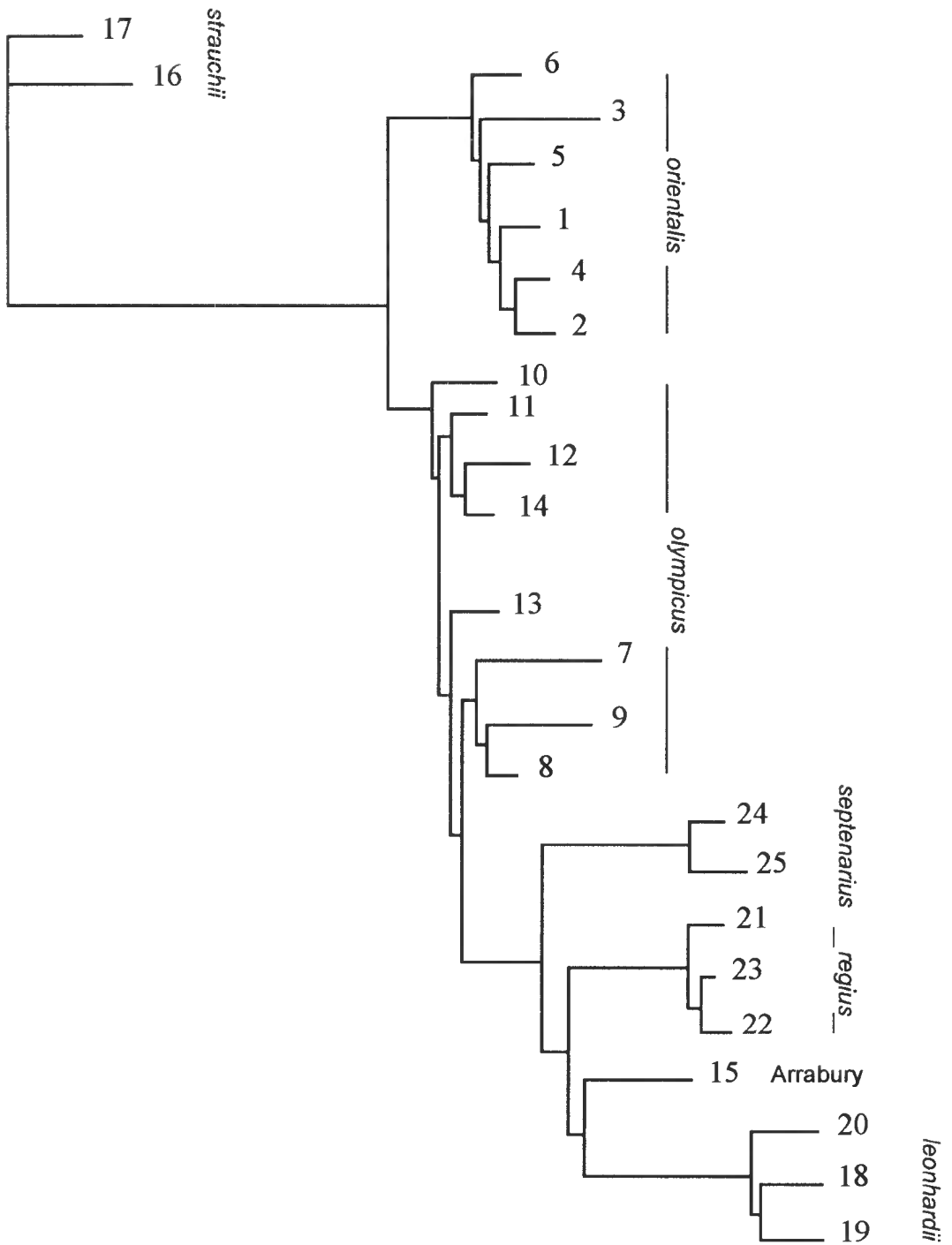
FIGURE 5. Phylogenetic relationships of 25 populations of *Ctenotus* skinks (analysis of Rogers' D using the FITCH algorithm from PHYLIP), showing paraphyly of *C. olympicus*. *Ctenotus strauchii* was designated as the outgroup to root relationships among the remaining species, all members of the *C. leonhardii* species group.

in the north. In the Flinders Ranges and the stony hills of the Olary Spur and Barrier Range, many specimens are much darker than elsewhere, with dorsal colour dark blackish brown, as in *C. orientalis*.

The most distinctive populations, included here with some reservation, are those from the northeastern limits of the species' range in northwest New South Wales and southwest Queensland. The five specimens examined (SAMA R10044, R36877, R36986, AMS R32604, R69731) are distinctively marked with black paravertebral and laterodorsal black lines or series of flecks on the nape and shoulders. Four of the five also have almost no trace of a light dorsolateral line, having only a zone of pale speckling. Henle (1996) also pointed out the difficulties of identifying specimens from this area, and of the variation within the similar southwestern Queensland species, *Ctenotus astarte*. However, his figured specimen is more like our unassigned 'Arrabury' specimen (and *C. astarte*) than the five assigned here to *C. olympicus*.

This species is found on heavy soils, generally with a stony component and a ground cover of chenopods. On plains, the species digs a burrow under a stone or bush. In the north of South Australia it occurs on and around gibber rises, sheltering in natural holes and spaces under rocks. Sometimes the only *Ctenotus* where it occurs, but often found with *C. strauchii varius*, *C. leonhardii*, *C. septenarius* and *C. saxatilis* in central and northern South Australia. Sadlier and Shea (1989) figure and describe the habitat of this species as *C. uber orientalis*. The photographs illustrating *C. uber* in Swan (1990, p. 96) and Ehmann (1993) also depict specimens of *C. olympicus*.

DISCUSSION

Our revised taxa are species because they are diagnosable, show evidence (fixed allozyme differences) that reticulate evolution has ceased between them, and maintain their morphological distinctiveness in sympatry (Wiley 1981, Frost & Hillis 1990). We cannot demonstrate reciprocal monophyly of these species, however, so that one of the current species concepts, the Phylogenetic Species Concept (PSC, de Queiroz & Donoghue 1988; Echelle 1990), cannot be applied. Failure to establish strict monophyly of all species may be no more than we should expect if the prevailing

allopatric and sympatric speciation models are true. Our experience of cryptic species in several taxa (Hutchinson & Donnellan 1992; Donnellan *et al.* 1993) suggests that it is common for differentiation to be achieved by frequency shifts in the states of shared characters or fixation of polymorphisms (applicable to both allozyme and external morphological data) rather than the acquisition by each species of evolutionary novelties.

The taxonomy of this complex is still far from final resolution. The restricted concept of *Ctenotus uber* adopted here still encompasses considerable variation and suggests that detailed study may reveal further cryptic species within this binomial. In eastern Western Australia, genetic study of populations assigned to *Ctenotus greeri*, *C. tanamiensis* and *C. uber* (including *C. u. johnstonei*) would help to unravel inter and intraspecific variation among these 'spotted-back' members of the *C. leonhardii* species group.

Three paratypes of *C. uber* from the vicinity of Mungilli Claypan (WAM R26894–95, R26897) all have the very long tail of *C. uber*, but R26897 is otherwise identical in colour to typical South Australian *C. olympicus*, while the other two are more like *C. uber* but have anomalous dorsal patterns, with relatively broad vertebral stripes and broad paravertebral zones of ground colour margining straight-edged laterodorsal stripes containing pale markings that run together to form ragged longitudinal pale lines. At present, we allocate R26897 to *C. olympicus* and retain the other two in *C. uber* but further collection in this area to examine the range of local variation will be necessary to clarify the status of these populations.

There are also several central and eastern-inland species, such as *Ctenotus aphrodite*, *C. astarte*, *C. hebetior*, *C. septenarius* and *C. serotinus* in which interpopulation variation is poorly understood and which may be closely related to *C. orientalis* and *C. uber*. One of these, *C. septenarius* is a more widespread and variable species than is indicated by the original description (King *et al.* 1988), and was included by Storr in the type series of both *C. uber* and *C. u. orientalis*. In the type series of *C. septenarius*, the dorsal colour pattern includes seven dark lines, a broad vertebral, a faint paravertebral and laterodorsal on each side and a wider dorsolateral. The two faint lines are the result of a single dark laterodorsal line on the nape developing a pale centre as it runs posteriorly but in many South Australian specimens the laterodorsal line does not fade as it runs back, so

that the resulting pattern consists of five bold dorsal lines, rather than three bold and four faint lines. Whatever the pattern it generally fades posteriorly, often reducing to three lines and then one (vertebral) on the posterior third of the back. A minority of specimens have only a vertebral line. *Ctenotus aphrodite* from southwest Queensland appears to be very similar to the single-lined pattern variant of *C. septenarius*, while some specimens of *C. astarte* and *C. serotinus* are similar to *C. olympicus* and to our distinctive Arrabury specimen. Future work should aim to sample these populations for biochemical or molecular systematic study.

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APPENDIX

The following specimens were used in the electrophoretic study and scored for morphological data (all locations but one in South Australia).

Ctenotus orientalis. population 1: SAMA R27220, Hensley Scrub, 8 km NW of Bordertown; population 2: R26069–71, Swan Reach; R26164, R26166, Swan Reach Conservation Park; population 3: R26184, White Dam Conservation Park; population 4: R18275–79, Reevesby Island; population 5: R24797, Pitcairn Station; R24875, Ti Tree Well, Flinders Ranges; R24876, 'The Bunkers', Flinders Ranges; population 6: R25074, Stoney Creek.

Ctenotus olympicus. population 7: R18620, approx. 20 km S of Port Augusta; population 8: R25877, Witchelina Station, near homestead; population 9: R28494, R28503, R28517, R28543, 115–120 km NE of Minnipa; population 10: R20936, Olympic Dam area; R20944–45, R20949, 48 km S of Olympic Dam; population 11: R30407, Breakaways Reserve, 25 km NNW of Coober Pedy; population 12: R35937, 95 km E of Marla; population 13: R36360, 1 km NE of Alberrie Creek; population 14: R28203, 37 km N of Oodnadatta on road to Hamilton homestead.

Ctenotus sp. population 15: R20839, Arrabury Station, Qld.

Ctenotus septenarius. population 16: R35895–96, R35931–32, Finke River valley, Witjira National Park; population 17: R28214, Dalhousie ruins.

Ctenotus leonhardii. population 18: R35878, Finke River valley, Witjira National Park; population 19, R28244–45, 'Big Mill' area, Witjira National Park; population 20: R22246, Kingoonya.

Ctenotus regius. population 21: R35860, R35938: 1 km S of Hamilton homestead; population 22: R35915, Mokari, Witjira National Park; population 23: R35940, Finke River valley, Witjira National Park.

Ctenotus strauchii varius. population 24: R35887, 26 km ESE Mt Dare homestead, Witjira National Park; R35889–90, Mt Dare homestead metal dump; population 25: R34780, South Gap Station.

Additional specimens which provided scalation and mensural data.

Ctenotus uber. R17335, 24 km SSE of Karonie (Paratype); R17654, 35 km SSE Yalgoo (Holotype); R25118, Jiggalong (Paratype); R26894–95, Mungilli Claypan (Paratype); R30334, Koordarrie; R33967, 46 km S of Karalee; R36112, 18 km SW of Winning Pool; R40216, S of Carnarvon Ranges; R40537–38, R40539–42, Yinnietharra, Mica Well; R44246, 46 km NNE of Beacon; R47708, Weedarra, Gascoyne River; R48323, 48 km N of Beacon; R48402, 51 km N of Beacon; R49945, Wandagee; R54209, Tallering; R57692, Wilroy Reserve, 19 km S of Mullewa; R58155, 12 km NE of Dalwallinu; R58697, 13 km SE of Diemals; R62303, 5 km N of Jindabinbin rockhole; R63664, 25 km NNW of Winning HS; R64742, Mt Manning Ra.; R65814, 7.5 km NE of Comet Vale; R65910, 3 km NE of Mt Linden; R65976, 2.5 km [from] Mt Linden; R67017, 1.5 km S of Mt Jackson; R67133, 5 km N of Bungalbin Hill; R67983, Hell Gates, 37 km 87° from Dandaraga HS; R68889, 2 km N of Mt Narryer HS; R71822, 16.5 km 80° from Toomey Hills; R71824, 15 km 90° from Toomy Hills; R72017, 1.5 km W of Mt Jackson; R72201, R76231, 12 km NNE of Bungalbin Hill; R72584, near Comet Vale; R72645, 7.5 km NE of Comet Vale; R72733, 6.75 km NE of Comet Vale; R72792, 2.5 km N of Mt Linden; R73287, R73308, 7 km 238° from Black Flag; R73222, 2 km 97° from Yowie rockhole; R73373, 1 km 260° from Mt Manning Ra. (SE peak); R74400, Boorabbin; R76095, Mt Jackson Hill; R76119, 12 km SSW Mt Jackson Hill; R78517, 7 km WSW of Black Flag; R78541, 12 km WSW of Black Flag; R78700, 2 km NW of Mt Manning Ranges (SE peak); R78777, 16 km E of Toomey Hills; R78796, 15 km E of Toomey Hills; R78810, Boodarding Rock; R81301, Koordarrie HS; R81965, Chiddarcooping nature reserve; R82623, 15 km SSE of Mt Jackson; R84146, 17 km SSW of Muralgarra HS; R87655, 13 km SSW of Mt Phillip HS; R87758, 4 km NNE Mt Phillip HS; R91036, 9 km N of Yinnietharra.

Ctenotus olympicus. South Australia: SAMA R02789, R09466–69, Pernatty or South Gap Homestead (Paratypes of *Ctenotus uber orientalis*); R04314, Ediacara; R10017 (Paratype of *Ctenotus uber orientalis*); R10027, R10030, Mern Merna (Paratypes of *Ctenotus uber orientalis*); R12845, near Carrapateena Arm, Lake Torrens; R12846, Wirrappa Hills, 29 km SE of Woomera; R12847, Yarra Wurta cliff, north end of Lake Torrens; R13156 B, near Oulnina HS, Olary Ridge; R13912 8 km from Carriewerloo Woolshed on road to Illeroo; R14160 A–B, R14917 A–C, Waukaringa; R14932, Mern Merna; R15111, Disputed Creek; R15439, 10 km SW of Matin Wells Homestead; R16082, Mt Serle; R17789, Dutton Bluff, 17 km ESE of Bookaloo; R17799, Wooltana Station, 4–Mile Creek Bore; R19026–27, 10 km N of New Mulgaria Homestead; R19048, 15 km E of Frome Downs Homestead; R20039–40, Pimba; R21518, Moolawatana; R26828, 25 km S of Mabel Creek Homestead; R28403, 28 km NW of Iron Knob; R29072–73; 128 km ENE of Minnipa; R29083, 130.8 km ENE of Minnipa; R33282, 14 km W of Pimba.

WAM R64576, Pimba. Northern Territory: SAMA R10055. (Paratype of *Ctenotus uber orientalis*). New South Wales: SAMA R10044, Milparinka; WAM R92962, 2 km E of Mungo HS. Western Australia: WAM R26897, 18 km E of Mungilli Claypan (Paratype of *Ctenotus uber*)

Ctenotus orientalis. South Australia: SAMA R00023–24, Bowhill (Paratype); R03618, Lake Palankarinna (Paratype); R05738, Panaramitee Station (Paratype); R01507, Pinnaroo (Paratype); R10122, Blue Range Creek (Paratype); R11202, 1.6 km NE of Tea Tree Gully; R12718, Artimore Station; R12986, Reeveshy Island; R14569, Marble Range, Eyre Peninsula; R15390, Wilpena Pound; R16225, Ninety Mile Desert; R18224, 6 km N of Cook; R18488, Reevesby Island; R20868, Stony Point; R21490, N end of Younghusband Peninsula; R24797, Pitcairn Stn; R26118–19, Reevesby Island; R28425, 37.5 km NE of Minnipa; R31453, Wardang Island; R35384, Reevesby Island. WAM R9863, Reevesby Island. New South Wales: AMS R92239, 6 km along Cambalong Rd, Bombala (Holotype of *Minervascincus monaro*).Victoria: NMV D00825, Ouyen (Holotype). Western Australia: WAM R17268, Forrest (Paratype of *Ctenotus uber*); R17284–

85, Seemore Downs (Paratype of *Ctenotus uber*); R41592, 92 km NNE Rawlinna; R41593, 39 km S of Forrest; R41594, 24 km S of Forrest; R45615, 22 km N of Rawlinna; R77772, 32 km NW of Toolinna rockhole; R77777, 25 km N of Eyre Homestead; R91322, 3 km S of Haig; R91324, R91327, R91761, R91770, 7 km ESE Kilidwerinia Granite Rock; R91326, R91328, R92001, 16 km SSE of Haig; R91595, 18 km S of Haig; R91748, 13 km SSE of Haig; R91753–54, 1 km S of Haig; R91766, R91777, 5 km ESE Kilidwerinia Granite Rock; R91767, R91784, 15 km ESE Kilidwerinia Granite Rock; R92119, 50 km NE of Balladonia Hotel-Motel; R94707, Haig; R96723, 67 km N of Eucla.

Ctenotus septenarius. South Australia: SAM R09735, Dalhousie Homestead (Paratype of *Ctenotus uber orientalis*). Western Australia: WAM R20759, Pass of the Abencerrages, Rawlinson Range (Paratype of *Ctenotus uber*).

In addition, all specimens registered as *C. uber* from New South Wales, Victoria and Queensland in the NMV, SAMA and WAM collections (up to 1993), plus a large series from the AMS were examined and their identities revised and used to plot the distribution map (Fig. 3).